

## Oviposition on the Backs of Female Giant Water Bugs, *Abedus indentatus*: The Consequence of a Shortage in Male Back Space? (Hemiptera: Belostomatidae)

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Females of the subfamily Belostomatinae (Lauck and Menke, 1961) characteristically fasten their eggs onto the dorsum of their mates, the males subsequently carrying the clutch until hatching. The use of males as oviposition sites led R. L. Smith (1979a) to suggest that at times a female's reproductive output may more likely be limited by the availability of unencumbered males on which to oviposit than by her own egg production. If this is true, then a gravid female unable to secure a "free" male may opt instead to lay a small clutch on some alternative substrate rather than not lay at all. Recently, Kruse and Leffler (1984) have observed egg-bearing females in a population of *Belostoma flumineum*. In this note I report a similar observation for *Abedus indentatus*.

Of 706 sexually-mature adult females<sup>1,2</sup> of *A. indentatus* Haldeman examined from 3 May to 15 August 1983 at Deep Canyon Creek, Palm Desert, California, I observed three females bearing eggs on their dorsum. (Females are identified by the possession of two tufts of setae located mesally near the apical margin of the genital plate [Menke, 1960].) The first female was collected on 17 May and carried 13 eggs (2.9 mm each), the second female was collected on 31 May and carried 2 eggs (2.6 mm each), and the third female was collected on 6 June and carried 52 eggs (3.6–4.6 mm each). The third female was recaptured on 7 July carrying 27 eggs, 14 of which had hatched as indicated by the presence of 14 empty chorions with ruptured cephalic caps (Smith, 1974). Whereas egg deposition on males begins at the apex of the hemelytra and proceeds forward, uniformly covering the dorsum of the male (Smith, 1974), the placement of eggs on the three females did not follow this pattern (see Fig. 1).

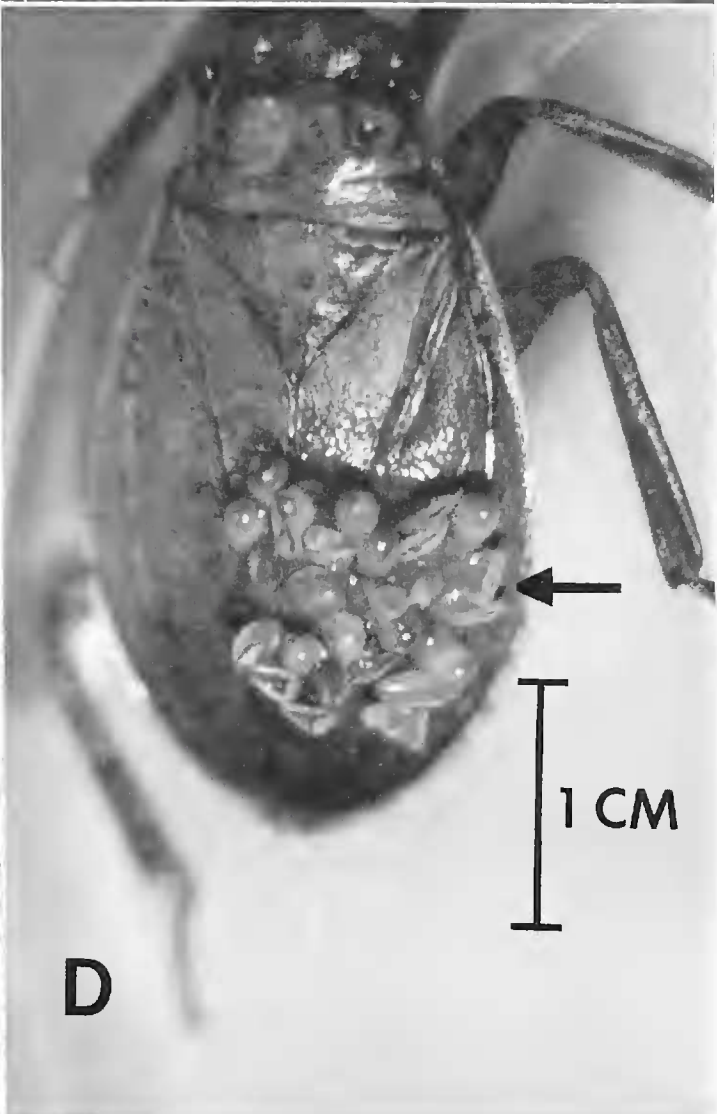
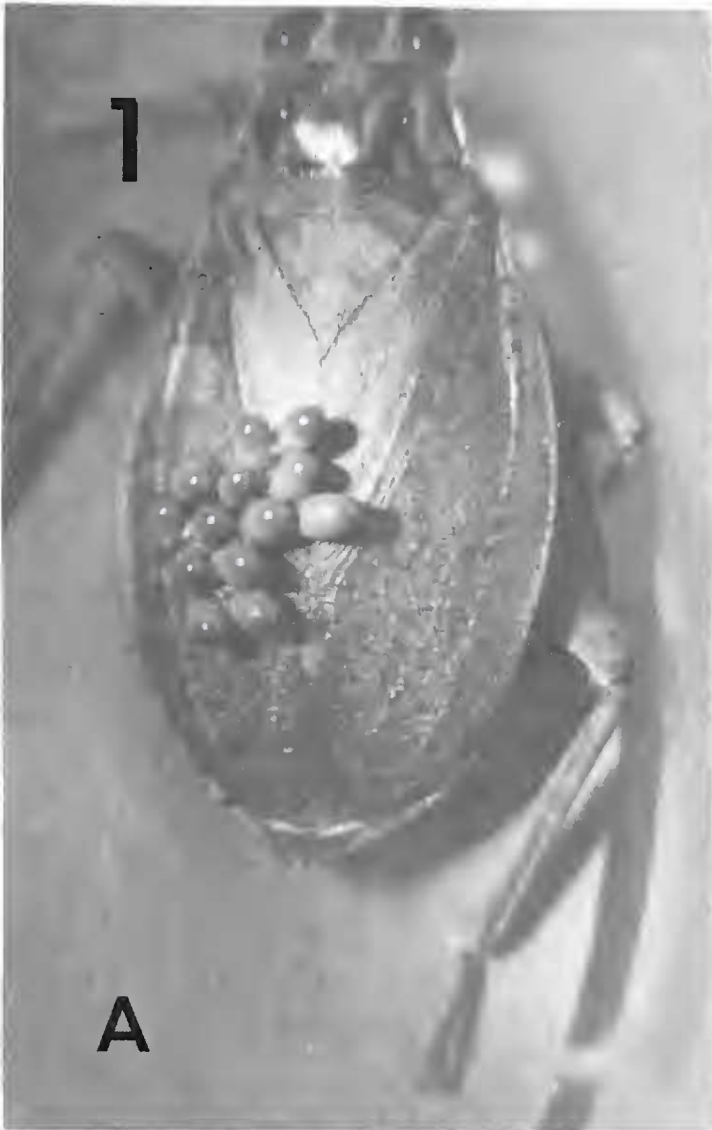
The fact that egg-encumbered females represent less than one percent of those examined in the field suggests that this phenomenon is quite rare. Since anatomical

<sup>1</sup> All individuals were marked for future identification, some individually with numbers on their pronotum, others simply by making a small cut in one hemelytron. All three of the egg-bearing females collected in the field had been individually marked.

<sup>2</sup> The 706 females represent females seen for the first time. None of the 229 recaptured females that was examined carried eggs. An additional sample of 672 recently-eclosed, sexually-immature adult females was not included here since it was uncertain as to whether their exoskeletons had hardened enough to bear eggs. No recently-eclosed male or female was ever seen carrying a clutch.

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Figure 1. Photographs of three egg-carrying females (A, B, C) collected at Deep Canyon Creek, California. Photograph (D) depicts the female shown in (C) 31 days later. Note the presence of empty chorions (arrow).





constraints preclude a female from ovipositing on her own dorsum, the eggs must necessarily be the product of a second female. Smith (1979a) has reported that heavily gravid female *A. herberti* will lay small clutches of eggs on floating aquatic vegetation in their containers. He suggested that this apparent relaxation in specificity for an oviposition substrate was due to a prolonged absence of the appropriate surface, i.e., an unencumbered male. I have seen similar behavior in *A. indentatus*, and Menke (1960) has demonstrated that a gravid *A. indentatus* female will oviposit at least a few eggs on the back of a male of a different species if a conspecific is unavailable. In addition, I have observed two instances of egg carrying by females in the laboratory (clutch sizes of 9 and 3 eggs, respectively), both instances occurring in aquaria containing only females. Although neither of these encumbered females were successful at rearing the clutch (both clutches were discarded before the eggs could hatch), one of the eggs deposited on the female carrying three eggs expanded to 5.6 mm before it was lost. A well-developed embryo was found when the discarded egg was dissected.

Judging by their size, the eggs on the three *A. indentatus* females collected in the field were laid in May and June 1983, months in which the majority of sexually-mature *A. indentatus* males carried broods (86.44%,  $n = 59$ , and 74.55%,  $n = 55$ , respectively). In addition, the adult sex ratio during the same period appeared to be significantly skewed towards females.<sup>3</sup> (Interestingly, Kruse and Leffler [1984] indicate that a majority of *Belostoma flumineum* males were also encumbered when they made their observations.) I therefore suggest that egg-encumbered females are the consequence of at least a temporary shortage in available male back space. It remains unclear as to whether females are simply renewing their oviducal egg supply until "free" males become available (Smith, 1979a), or whether they are attempting to rear a small brood in the absence of such males. In regards to the latter hypothesis, I agree with Kruse and Leffler (1984) that this phenomenon is not an alternative to male brooding. However, it may be a viable option in instances where males are locally unavailable and when the only other alternative is not to lay at all. Finally, although egg-encumbered females could conceivably be the result of recognition errors made by ovipositing females, the complexity of courtship that characterizes *Abedus* (Smith, 1979a; Kraus, pers. obs.) makes this hypothesis unlikely.

Smith (1979b) has convincingly argued that the repeated bouts of copulation observed in *Abedus* are an adaptation to assure paternity through sperm precedence. The presence of hatched eggs on the back of the female recaptured in July demonstrates that the potential for cuckoldry does exist in nature, since the fertility of these eggs was dependent on the ovipositing female having retained at least some viable sperm from a previous mating. In addition, although male-specific brooding behaviors such as broodpumping appear to significantly increase the hatching success of a brood (Smith, 1976a, 1976b; Venkatesan, 1983), they are apparently not essential for egg development. In fact, the low survival rate of female-borne clutches may be as much a result of the irregular placement and small sizes of these clutches as it is a consequence of the disparity in brooding

<sup>3</sup> The sex ratio of previously unmarked, sexually-mature adults closely fit a 2:1 ratio in favor of females ( $n = 263$ ,  $\chi^2 = 0.008$ ,  $df = 1$ ,  $P > 0.9$ ). Sampling bias in catchability, analyzed over a 2-week period subsequent to marking, could not be detected ( $n = 103$  recaptures,  $\chi^2 = 0.60$ ,  $df = 1$ ,  $P > 0.2$ ).

behaviors between the sexes. Even among males, small clutches appear to be much more susceptible to losing their adhesion and being discarded than large ones (especially when expansion of the developing eggs increases drag). In this regard, it is suggestive that the one field-collected female which was observed to have successfully reared a clutch also carried the largest number of eggs.

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